Systematic Position and Biology of *Pectinatella gelatinosa*Oka (Bryozoa: Phylactolaemata) with the Description of a New Genus

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ABSTRACT—The biology of "Pectinatella" gelatinosa is reviewed, and it is proposed to establish the new genus Asajirella for Pectinatella gelatinosa Oka, 1891. The new genus is closely related to Lophopodella, but differing from it in forming composite colonies and nearly square saddle-shaped statoblasts. Asajirella, together with Lophopodella and Lophopus, should be placed in the Lophopodidae, and is regarded as the most specialized genus of these three. A discussion on the phylogenetic relations among higher phylactolaemates is also given. The families Pectinatellidae and Cristatellidae are closely related to each other, but they are distantly related to the Lophopodidae.

INTRODUCTION

Pectinatella gelatinosa was originally described by Oka [1] in 1891 based on the material obtained from Shinii Pond on the campus of the Imperial University of Tokyo. At that time, he assigned this species to the genus Pectinatella based on the massive growth form of the colony, the copious hyaline gelatinous nature of ectocyst, and the formation of saddle-shaped floatable statoblasts with marginal hooks. These characteristics are shared with the previously characterized species. P. magnifica (Leidy), the other member of the Pectinatellidae. However, recent studies on the histological and histochemical features of the epidermis [2], the morphology of the statoblasts [3, 4], the growth pattern of colonies [5], and the karyotype [6] all indicate that P. gelatinosa is more closely related to Lophopodella, especially L. carteri (Hyatt), than to P. magnifica. On the other hand, the species in question is different from Lophopodella in some other important characteristics. Thererore, it is reasonable to establish a new genus for P. gelationsa.

In this paper, descriptions of the new genus and the biology of "gelatinosa" are given, and a discussion on the phylogenetic relationship among higher phylactolaemates is also comprised.

SYSTEMATIC ACCOUNT

Asajirella gen. nov.

The colony proper is massive and oval in outline, with a dichotomously branched, sac-like cystidal wall; no septa between the cystids; ectocyst copious, colorless, hyaline and gelatinous, covering thinly even the dorsal side of the cystid, and forming a common base for many colonies; polypides most crowded in the periphery of the colony; digestive tract straight when retracted; statoblast (floatoblast only) large and nearly square to somewhat oblong with rounded corners as it lies flat, curved in two axes like a saddle, with numerous minute marginal hooks, and non-buoyant unless dried; larvae bear as a rule two polypides.

This new genus is diagnostically distinguished from *Pectinatella* Leidy, 1851 [7] in forming saclike colonies and non-buoyant floatoblasts, and from *Lophopodella* Rousselet, 1904 [8] in forming large gelatinous aggregation of colonies and nearly square saddle-shaped flaotoblasts. As will be

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¹ Present address: 5-27-15 Kugayama, Suginami-ku, Tokyo 168, Japan. discussed below in detail, this new genus is more closely related to *Lophopodella* than to *Pectinatella*, and should be placed in the family Lophopodidae.

Etymology: This genus name is named after Asajiro Oka (1868–1944), who was one of the excellent zoologists, and who first studied freshwater bryozoans in Japan, with a diminutive, -ella.

Type species: Pectinatella gelatinosa Oka, 1891.

Asajirella gelatinosa (Oka, 1891), comb. nov.

Pectinatella gelatinosa Oka, 1891 [1]; Toriumi, 1941 [9]; Toriumi, 1956 [10]; Lacourt, 1968 [11].

Pectinatella burmanica Annandale, 1908 [12].

For the time being, this is the only species belonging to the genus Asajirella.

BIOLOGY OF Asajirella gelatinosa

Colony

A colony or zoarium is externally circular to somewhat oval, measuring about 1.5–2.5 cm in diameter. There are no septa between zooids, and the cystids of all zooids are united to form colonial wall (or coenoecial endocyst) enclosing a common body cavity in which polypides are suspended. Polypides are most crowded along the margin of

the colony, and arranged with their oral or ventral side facing outward. In the central part of the colony, functional polypides are scarce, and some club-shaped protrusions, which represent the cystids of degenerated polypides, are present (Fig. 1A). The colony is sac-like, with the conically protruding basal wall, so that the polypides can retract with their digestive tracts straight.

When the colony is observed from the underside, the dichotomous branching pattern of radially-arranged short branches, with some deep constrictions between them, is clear. The budding zone is restricted to the basal margin of the colony or to the ventral side of marginal zoneids. Along the basal submarginal zone of the colony, there are some adhesive pads or attachment organs of the colony consisting of specialized epidermal cells, the alveolar cells [2, 13].

The ectocyst is colorless, hyaline and gelatinous. It is thick basally, and covers the surface of the colony in a thin coat. As a rule, the copious ectocyst makes a common base for many colonies (Fig. 1B). The composite colonies often reach about 15 cm across and 30 cm long.

Polypide

The polypide is essentially the same in gross morphology with those of other species, but it is the largest in phylactolaemates, measuring about 5





Fig. 1. Colonies of Asajirella gelatinosa gen. et comb. nov. A. Single colony, about 1 cm in diameter. Functional polypides are crowded along the periphery; several club-shaped cystids of degenerated polypides are seen in the central part. This colony was collected from a pond on the Imperial Villa of Katsura, Kyoto. B. Massive gelatinous aggregation of colonies, about 25 cm long, growing at the bottom of water in Lake Ezu, Kumamoto.

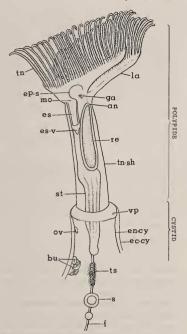


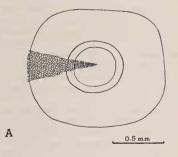
Fig. 2. Diagrammatic representation of the polypide of Asajirella gelatinosa. Retractive muscles are not shown; the collar-like distal part of the cystid is shown an, anus; bu, bud; ec.cy, ectocyst; en.cy, endocyst; ep.s, epistome: es, esophagus; ex, esophageal valve; f, funiculus; ga, ganglion; la, lophophore-arm; mo, mouth; ov, ovary; re, rectum; s, statoblast; st, stomach; tn, tentacle; tn.sh, tentacular sheath; ts, testis; yp, vestibular pore.

mm in length (Fig. 2). The digestive tract is Y-shaped in side view. The lophophore is horseshoe-shaped, bearing long, ciliated tentacles along its margin. The number of tentacles is mostly 90–98 [1], ranging from 75 to 106 [10]. When expanded, all parts of the digestive tract in grown polypides are wholly surrounded by the tentacular sheath, but in younger polypides a posterior portion of the stomach remains within the cystidal tube projecting above the body of the

colony. The digestive tracts are almost straight even when retracted. Oda [14] found that a sudden retraction of polypides causes the ejection of coelomic fluid, together with a number of coelomic corpuscles and spermatozoa, through the vestibular pore at the dorsal upper margin of the cystidal tube. For histological and histochemical features of the polypide, see Oka [1] and Mukai [15], respectively. A double monster with completely separate polypides, belonging to the oral type, has been reported [16, 17].

Statoblast

Only the floatoblast is produced (Fig. 3A). It is somewhat oblong or nearly quadrate with rounded corners, measuring about 1.5×1.3 mm in size and about 0.3 mm in thickness [1]. The cystigenic or dorsal side and the deutoplasmic or ventral side can be distinguished. The annulus has double curvature like a saddle. On the cystigenic side, it is convex along the major axis and concave along the minor axis. Both surfaces of the statoblast are beautifully marked into hexagonal meshes, the diameter of which decreases as one approaches the center. The central capsular area, the so-called



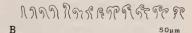


Fig. 3. Statoblast of Asajirella gelatinosa. A. Cystigenic side of a statoblast. B. Various types of hooks emerging from the rim of the deutoplasmic valve.

fenestra [18], is oval on the cystigenic side and circular on the deutoplasmic side. The statoblast does not float unless it is dried. Once dried, however, the float chambers of the annulus are filled with air and the statoblast floats on the surface of the water with the cystigenic side up.

The shell consists of two valves, which are separated from each other when the statoblast germinates. When flattened, the cystigenic valve is oval and the deutoplasmic valve is circular, the diameter of the latter being intermediate between the length and width of the former [3]. Numerous minute hooks are present around the margin of the deutoplasmic valve. They rise from the edge of the valve, and have no direct connection with the central part. The shape of the hooks varies widely; some of them are complex, while others are simpler (Fig. 3B).

In cross-section, the shell is found to consist of three layers, from within to the outside, the inner chitinous layer representing the capsule, the outer chitinous layer forming the walls of the float chambers, and the basophilic layer covering the surface of the statoblasts [3]. The latter two layers enveloping the central capsule form periblast [18]. When the statoblast is treated with 10 M KOH at room temperature, the periblast is separated into two valves, cystigenic and deutoplasmic, leaving the capsule intact and the germinal mass within the capsule still viable [19]. Each lateral wall between float chambers is provided with one small pore which is simple in structure [3]. The formation of the shell and its architecture have been studied by transmission as well as scanning electron microscopy [4, 20].

The germinal mass is composed of two parts, an outer layer of epidermal cells and an inner mass of yolk cells. The yolk granules are uniformly small and oval with a length of about 2 μ m [3]. The yolk cells have been studied histochemically [21] and electron microscopically [22, 23].

In nature, young colonies appear from overwintered statoblasts in early summer. The colonies produce numerous statoblasts from mid-summer to autumn. Mature statoblasts are set free from the funiculus and accumulate in the coelom (Fig. 4). The statoblasts are released after the disintegration of colonies in late autumn, when they are

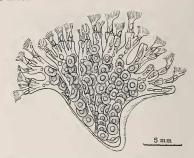


Fig. 4. Ventral biew of a colony of Asajirella gelatinosa collected from Furutone-numa, Chiba Pref., in late autumn. The coelom is full of mature statoblasts.

in a dormant state [24]. These statoblasts survive the winter and germinate in the early summer of the following year.

Sexual reproduction

Oka [1] described the ovary, but no testis. The testis was found first by Oka and Oda [25]. Spermatozoa have been illustrated in Oda and Nakamura [26], and oogenesis has been studied by Tajima et al. [27]. According to Annandale [28], in Lower Burma many larvae were produced. In Japan, Oda and Nakamura [26] found only four larvae among a number of colonies obtained from Furutone-numa (Chiba Pref.) in August, 1962. The larva is oval or spherical, about 1.2 mm in diameter, and has two grown buds of slightly different sizes. At Tatara-numa (Gunma Pref.), both testes and ovaries are produced in the summer season, but no larvae have been found [13, 24]. Therefore, at least in Japan, sexual reproduction of the present species seems to be very limited.

Budding and colony formation

The budding zone is located on the ventral wall of the zooid. Blastogenesis has been studied in detail by Oka [1]. Mukai *et al.* [5, 13] studied the mode of budding and colony formation, starting from the ancestrula germinated from a statoblast. As a rule, the ancestrula produces three buds, and each of the subsequent zooids produces two buds.

not simultaneously but successively. The paired buds are located bilaterally relative to the median sagittal plane of the mother. A left bud always produces its first bud to the right, and vice versa. As daughter zooids separate rather laterally away from their mother zooids, thus leaving traces of dichotomous branching, a young colony is fanshaped with zooids and buds occupying the peripheral arc. Subsequently, the colony becomes semicircular and then circular. With continued budding, the colony becomes oval in outline and is eventually divided into two or more small colonies.

Karyotype

Five different karyotypes have been found in germinating statoblasts obtained from Tataranuma. The five karyotypes are consistent in having 18 chromosomes, showing that the 2n is 18 [6].

Distributions

The present species has been recorded from Japan [1], Burma, India [12, 28], Java [29], Korea [30] and Taiwan [31].

Within Japan, this species has been distributed widely in the southern half [10]. A number of localities have been recoreded in the Kanto district, but at the present time we can find no colonies in the city of Tokyo. Mukai [21] reported the abundant occurrence of colonies in Tataranuma (a pond), Gunma Pref., and most recent studies have utilized material collected at this pond. More recently, the occurrence of this species has been known in Lake Ezu, Kumamoto Pref. [32], a pond in Mitsukaido, Ibaraki Pref. [33], a reservoir in Kurashiki, Okavama Pref. (personal communication of 1986 from Dr. Kuniyasu Satoh, Kawasaki Medical College), Isanuma, Saitama Pref. and a pond on the Imperial Villa of Katsura, Kyoto [34].

PHYLOGENETIC RELATIONSHIPS OF HIGHER PHYLACTOLAEMATES

Lophopus, Lophopodella and Asajirella have several characteristics in common, e.g., sac-like colonies with the convex basal wall [5, 35]; ectocyst covering the whole cystids; PAS-negative vacuolar cells and PAS-positive alveolar cells in the

epidermis [2]; non-buoyant floatoblasts with a three-layered shell and small yolk granules [3, 4]; and larvae with two grown buds [26, 36]. Moreover, *Lophopodella* and *Asajirella* have similar karyotypes [6]. Therefore, these three genera should be placed in the same family, the Lophopodidae.

The genus Lophopus consists of a single species, L. crystallinus (Pallas), in which the colony is semicircular [35] and the statoblast is spindle-shaped with pointed ends [3]. In Lophopodella, individual colonies are separated and statoblasts are generally elliptical with marginal hooked spines. Asajirella produces aggregations of colonies and nearly quadrate statoblasts with minute hooks around the margin of the deutoplasmic valve. Thus, Lophopus seems to represent the least specialized type and Asajirella seems to be the most specialized in the Lophopodidae.

The genus Lophopodella comprises four distinct species: L. capensis (Sollas), L. thomasi Rousselet, L. carteri (Hyatt), and L. pectinatelliformis Lacourt. A series of changes in the number and position of the spines can be seen among these species. The statoblasts of L. capensis have a single hooked spine at both ends [4, 37], and those of L. thomasi are furnished with 3 or 4 hooked spines at both ends [4, 8, 37]. Statoblasts of L. carteri show markedly seasonal changes [38]. The number of hooked spines at one end is usually 6 to 16, but varies from 1 to 25. The dimensional outline of the statoblast proper also changes from spindle to elliptical to square and then circular as the number of spines increases. This variation depends mainly on the water temperature [38, 39]. At high temperatures (up to 30°C) the statoblasts are spindle-shaped with one to a few spines at both ends. The number of spines definitely increases with decreasing temperature. Statoblasts nearly circular in shape and bearing large numbers of spines along the entire border are formed at 10°C. The spindle-shaped statoblasts with one spine at both ends resemble those of L. capensis, and the spindle-shaped statoblasts with a few spines at both ends resemble those of L. thomasi. The statoblasts of L. pectinatelliformis are ellipsoidal in shape and have a number of minute anchor-like hooks emerging from the entire borders of both

valves [11, 40], thus more or less resembling the circular statoblasts with numerous spines of *L. carteri*. Accordingly, *L. pectinatelliformis* should be an intermediate between *L. carteri* and *A. gelatinosa* in terms of statoblast morphology.

The genus Pectinatella was established by Leidy [7], and now comprises an only species, P. magnifica (Leidy), which was originally described as Cristatella magnifica Leidy [41]. Cristatella also currently comprises a single species, C. mucedo Cuvier. In these two genera (and species), the colony is flat so that the digestive tracts of the polypides, when retracted, are folded characteristically [5], and the ectocyst covers only the basal wall [2]. Their statoblasts are buoyant with the annulus developed more voluminously on the cystigenic valve than on the deutoplasmic valve, and no distinction between the capsule and the periblast is possible [3]. Their larvae have generally four grown buds [see 42-44]. In these respects, these two genera are clearly distinguished from the members of the Lophopodidae. In some respects Asajirella does resemble Pectinatella. In both genera, colonies form massive aggregates, and statoblasts are saddle-shaped. These resemblances seem to be superficial without phylogenetic significance.

In Pectinatella, the colony is rosette-shaped and radially branched or lobulated; a number of colonies form a huge gelatinous mass. The statoblast of this genus is somewhat oblong in outline, saddle-shaped, and bears spines emerging only from the cystigenic valve. On the other hand, the colony of Cristatella is worm-like in shape and not lobulated. Its statoblast is circular with the equatorical annulus borne entirely on the cystigenic valve and spines arising from both valves. On account of these marked differences, Pectinatella and Cristatellidae should be placed in different families, Pectinatellidae and Cristatellidae, respectively. The family Pectinatellidae was erected by Lacourt [11] to comprehend both Pectinatella mag-

Cristatellidae

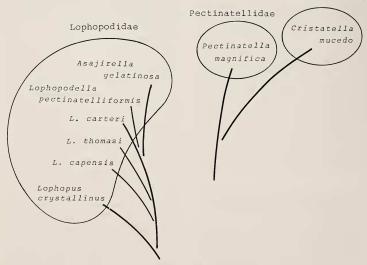


Fig. 5. Phylogeny of higher phylactolaemates.

nifica and "P." gelatinosa, but now this family should be amended to comprise only a single species, P. magnifica. The Cristatellidae seem to be more specialized than the Pectinatellidae.

On the basis of the above discussion, we propose a phylogenetic relationship of higher phylactolaemates in Figure 5. Our proposition is essentially consistent with that presented by Mukai [44], but is different in some important points from those by Toriumi [45] and Lacourt [11].

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